

MENISCATE TRACE FOSSILS AND THE *MUENSTERIA-TAENIDIUM* PROBLEM

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ABSTRACT. The systematics of meniscate trace fossils are in need of revision. Most authors follow Seilacher and call unbranched, unlined meniscate burrow fills *Muensteria*. However, Sternberg's original description of *Muensteria* is highly confused, involving true algae, a coprolite, and forms of *Chondrites*, and the name cannot be considered available for trace fossils. Re-examination of the original description of *Taenidium* Heer has revealed that the earliest ichnospecies erected, *T. serpentinum*, corresponds closely to the forms called *Muensteria* in the more recent literature. Subsequent ichnospecies placed in *Taenidium* include septate branched forms that require a new name. It is these branched meniscate burrows that commonly have been referred to *Taenidium*. We designate the branched forms *Cladichnus* ichnogen. nov. on the basis of *T. fischeri* Heer. *T. satanassi* ichnosp. nov. is described from the lower Tertiary of Italy. Other ichnogenera of meniscate trace fossils are briefly discussed, including *Nereites*, *Keckia*, *Scolicia*, *Psammichnites*, *Scopyenia*, *Beaconites*, *Phoebichnus*, and *Ancorichnus*.

TRACE fossils having a cylindrical form and meniscate structure are common in many settings. Generally they represent the active packing of sediment behind animals moving through the loose substrate for food, or vertical escape traces. Although meniscate structures are particularly characteristic of shallower marine deposits, they also occur in continental and deep marine basinal settings. Authors today tend to follow Seilacher (1958, 1962, 1964) in considering that *Muensteria* embraces these 'stuffed linear burrows', but this conflicts with the original diagnosis of Sternberg (1833, p. 31): '*Frons coriacea, fistulosa, cylindracea aut simplex caespitosa aggregata, aut dichotoma, transverse elevato-striata, striis interruptis creberrimis. Sporangia punctiformis, sparsa, creberrima, inter strias laminae frondis immersa*' (Approximate translation: Leathery frond, pustulose, cylindrical, or simply aggregated as a bush, or dichotomous; transversely striated in relief, with dense, interrupted striae. Sporangia punctiform, scattered, very dense, immersed between the laminae of the frond.)

In contrast, '*Taenidium*' is generally used for branched meniscate structures, although this conflicts with Heer's (1877) original diagnosis: '*Frons cylindrica, fistulosa, plerumque simplex, rarius ramosa, annulata, dissepimentis instructa*' (Cylindrical fronds, pustulose, usually simple, rarely branched, annulated, provided with partitions.)

A close inspection of the status of these names is clearly overdue (see e.g. Frey and Howard 1985, p. 378).

STRUCTURE OF MENISCATE TRACE FOSSILS

There are several reasons for the confusion that at present characterizes the systematics of meniscate trace fossils. Among the most important is the heterogeneous nature of the taxobases used. These comprise: (1) a meniscate backfill, together with the presence or absence of (2) discrete wall structure, (3) wall ornament, and (4) true branching. Not all of these features are suitable or easy to use as diagnostic characters. Another cause of taxonomic difficulty is that many of the taxa were introduced as algae and were thus described in non-ichnological terms. These problems, of course, are far from restricted to the meniscate trace fossils, but are of general occurrence in older ichnological systematics (Pemberton and Frey 1982).

Backfill. Meniscate backfill occurs in many morphologically distinctive groups of trace fossils. It is considered an essential feature of such ichnogenera as *Ancorichnus* and *Scolicia*, but also occurs as an accessory feature, albeit rarely, in ichnospecies of *Ophiomorpha* and *Teichichnus* (Frey and Bromley 1985), *Chondrites*, and many others. As a basic result of any tunnelling that involved active stuffing behind an animal, meniscate backfill alone is not particularly suitable as an ichnological taxobase.

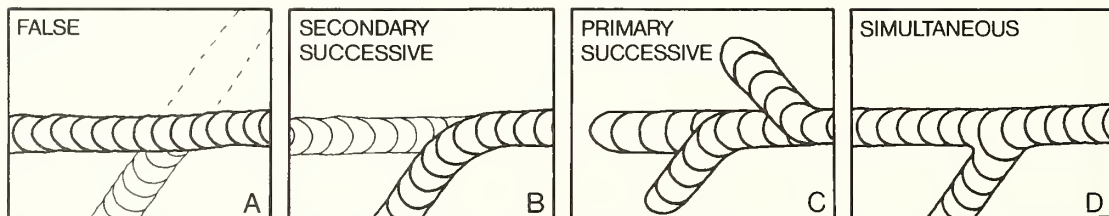
Wall structure. The boundary between burrow fill and undisturbed surrounding sediment may display a host of different features. The boundary may be defined by a clean discontinuity surface caused by a different grain orientation on either side of the junction (e.g. Heinberg 1973, 1974), or by a difference in consistency of the two sediments. Diagenesis may enhance this difference to produce a coloured halo or local concretionary effect. A thin film of clay minerals or carbonaceous material may occur at the boundary, but this is commonly difficult to detect and is lost in weathered material; we do not regard this film as a true 'lining'. Alternatively, the burrowing organism may have actively deposited a true lining on the open wall, as in *Ophiomorpha* ichnospp. (Frey *et al.* 1978), or the animal's burrowing technique may have produced a superficial zone around the periphery of the fill with a special construction, as in *A. ancorichnus* (Heinberg 1974). In these cases, therefore, the boundary is marked by a zone of sediment having a distinctive structure. Finally, local compaction of sediment caused by the construction of the burrow may have produced a preservable boundary feature. In a variable lithology, the characteristics of the burrow boundary may change locally, reflecting the original sediment consistency and consequent changes in burrowing technique. This is also the case for the scratch ornament, which may well be preserved in a firm, fine-grained lithology but is lost in a soft, coarse sand (Fürsich 1974, p. 22).

A corollary of this problem of substrate variation is that of preservation in general. The 'same burrow' may exhibit widely different morphologies in different preservational situations, e.g. in full relief within a sandstone, or epirelief at the sandstone boundaries. In some cases these widely different morphologies have been lumped together as a single ichnotaxon on the basis of their belonging to the 'same burrow' (see the *Scalarituba/Phyllodocites/Nereites/Neonereites* problem: Chamberlain 1971, 1978).

Branching. The main problem here is that of ramification. Burrows may branch in several distinct fashions (Bromley and Frey 1974, fig. 6):

A. On irregular rock surfaces, simple intersection of burrows can be mistaken easily for true branches (text-fig. 1A); this is particularly so where a high degree of compaction has brought burrows that originally lay at different levels in the sediment into close juxtaposition (text-figs. 2 and 3).

B. Commonly a deposit feeder reworks the backfill of a pre-existing burrow and then leaves the earlier course (text-fig. 1B) at an angle to produce a side branch. We suggest calling this type



TEXT-FIG. 1. Diagrammatic representation of four distinct modes of producing branched biogenic structures. A, false branching, where accidental intersections on an irregular surface can give the spurious impression of branching. B, secondary successive branching, where an animal followed the fill of an earlier burrow for some distance, giving the false impression of branched burrows. C, primary successive branching, where the same animal produced a systematically branched structure, actively filled. D, simultaneous branching, where a network of open burrows is produced; the simultaneous stuffing of both branches would produce this pattern, but it is a process that is presumably not possible.

TEXT-FIG. 2. *Taenidium satanassi* ichnosp. nov. Field photograph of material displaying the opposite colour-play to the usual: the pelleted sediment here is the paler. Scale, 1 cm.

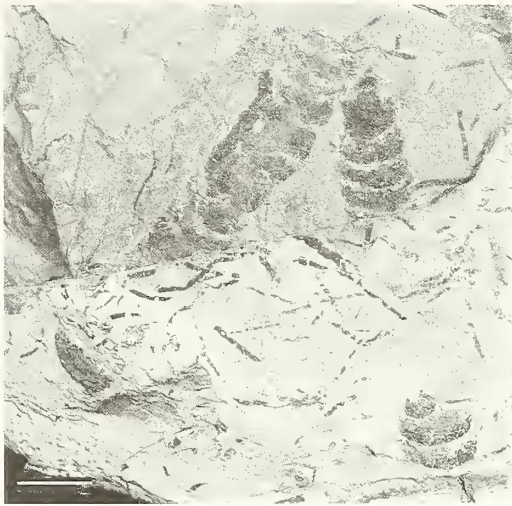


'secondary successive branching', as it is produced by two individuals in successive burrowing operations. In many such cases the direction of movement (meniscus orientation) is opposite in the two burrows, which reveals the type of structure immediately (e.g. Brady 1947, pl. 69, fig. 1; herein text-fig. 2). In other cases, however, where the menisci are concordant (e.g. Bromley and Asgaard 1979, fig. 10) it is not easy to distinguish this branching category from the next.

C. In burrow systems where successive probings are made after backfilling previous probes (e.g. *Chondrites*: Seilacher 1957, fig. 2; Ferguson 1965), a single individual produces a branched structure having a characteristic backfill pattern (text-fig. 1C). We call this type of bifurcation 'primary successive branching' (text-fig. 4).

D. Finally, where an open gallery is produced, side branches and dichotomous bifurcations exist simultaneously as empty habitations. This type we call 'simultaneous branching'. The fill might be emplaced either in successive operations, i.e. one branch filled at a time, as in *Ophiomorpha* (Bromley and Frey 1974, fig. 11), or alternatively, the two branches might be filled at more or less the same time. In the latter case, a backfill pattern is produced (text-fig. 1D), but although this structure has been illustrated in sketches (e.g. Seilacher 1955, fig. 5.83) it is not easy to understand the mechanics of the process. Probably 'simultaneous backfill' does not exist. It is easy to envisage this structure arising in a growing alga, however, the menisci representing successive terminations of the thallus (e.g. Fischer-Ooster 1858, pl. 7, fig. 3). We emphasize these difficulties because branching patterns play an important role in understanding the history of the taxonomy of meniscate trace fossils.

Algal origins. Most ichnogenera erected in the nineteenth century were initially described as body fossils of fucoid algae (Häntzschel 1975, p. 14). This fact renders interpretation of the initial descriptions very difficult, owing to the terminology used and the unintentional bias of original authors. 'Sporangia' usually may be interpreted as pellets, 'epithelia' as walling material, etc. A greater



TEXT-FIG. 3. *Taenidium satanassi* ichnosp. nov. showing false branching (cf. text-fig. 1A). Scale, 1 cm.

problem, however, is the tendency to assume that 'fucoid' fossils were branched in the same way as the extant seaweed *Fucus* (text-fig. 3), a tendency that was encouraged by discoveries of truly branched trace fossils (e.g. *Chondrites*). Thus even unbranched trace fossils such as *Cruziana* were described as branched, owing to the misinterpretation of intersections (Osgood 1975, p. 6).

Meniscate ichnotaxa share all these problems. On account of the 'branching bias', authors tended to regard crowded, intersecting trace fossils as more 'complete' than isolated ones, and secondary successive branching and false branching were readily interpreted as true ramifications. In this way, crowded or bunched trace fossils were selected for illustration, and consequently as type material, whereas in trace fossils such material preferably should be avoided. As explained above, branching in trace fossils is a complicated and critical matter; it is not sufficient merely to repeat the original author's statement regarding branching in algal terms when emending the diagnosis of a fucoid taxon in terms of trace fossils.

Taxobases for meniscate trace fossils

Ichnotaxa are based upon morphological features of trace fossils, primarily those that reflect behavioural qualities of the excavating organism. Morphology is also influenced, however, by external factors such as stratigraphic conditions and diagenesis. Such morphological features are unsuitable as taxobases and primary features reflecting behaviour should be chosen if possible (Seilacher 1953; Fürsich 1973; Bromley and Frey 1974). For example, as Smith and Crimes (1983) pointed out, *Scolicia* and *Subphyllochora* represent closely similar if not identical patterns of behaviour. Their preservation, however, is different—*Scolicia* being a concave epirelief and *Subphyllochora* a full relief expression of the same structure. Häntzschel (1975) suggested, therefore, that *Subphyllochora* be considered a junior synonym of *Scolicia*. In contrast, the structures *Ophiomorpha*, *Thalassinoides*, *Spongeliomorpha*, and *Gyrolithes* may all be found in mutual connection as a single burrow system (Fürsich 1973; Bromley and Frey 1974; Pemberton and Frey 1982); yet they represent different behavioural responses of the burrowing organism to environmental and biological factors, and so should not be placed in synonymy. In this way, the ichnotaxon unites behavioural patterns of the same type. This is not to question the importance of preservational aspects: taphonomic processes are closely linked to sedimentary facies and the dominance of a particular preservational style in an ichnotaxon in a given occurrence provides useful information on depositional environments.

CONCLUSIONS

The erection of several ichnogenera for the septate or meniscate trace fossils is clearly justified on the basis of their wall details and presence or absence of branching (see below): walled structures include *Phoebichnus*, *Ancorichnus*, and an unnamed branching group; unwalled structures containing longitudinal canals or ridges are distinguished as *Scolicia* and *Psammichnites*; *Nereites* has a unique disturbance zone around it, whereas *Scoyenia* has no wall but is ornamented by longitudinal scratches; *Beaconites* is dubious, having a weak wall or none at all, and it should probably be included in *Taenidium* as defined herein; *Keckia* appears to be a *nomen dubium* and is probably a heterogeneous taxon, including elements resembling several other taxa.

The unwalled meniscate trace fossils pose the greatest problem. *Muensteria*, in spite of the general use of this name today, must be regarded as unavailable for trace fossils. On the basis of its first ichnospecies, *Taenidium* is available for the unbranched ichnospecies of *Muensteria* of authors, and *T. serpentinum* remains its type ichnospecies. However, Heer's *T. fischeri* and *T. lusitanicum* must be transferred to the flabelliformly branched and annulated *Cladichnus* ichnogen. nov.

SYSTEMATIC PALAEOONTOLOGY

In our attempt to clarify the meaning of *Muensteria* and *Taenidium*, we reinterpret their original diagnoses in terms of ichnotaxobases and must therefore examine briefly the distinguishing features of related meniscate ichnogenera. We suggest synonyms among these ichnogenera (although we have not examined type material) which are treated below in chronological order.

Muensteria Sternberg, 1833

Discussion. Many authors have used the taxon *Muensteria* in recent years to define simple, unlined, unbranched meniscate structures (e.g. Seilacher 1962, 1964; Fürsich 1974; Chamberlain 1977; Pemberton and Frey 1984; Frey and Howard 1985), despite the fact that Häntzschel (1962, 1975) clearly demonstrated the weakness of the taxon. Thus, although *Muensteria* for these authors is a fairly well-defined concept, *Muensteria* Sternberg remains largely uninterpreted: it is, as Häntzschel (1975) stated, a heterogeneous genus.

Sternberg (1833) based his algal genus *Muensteria* on six species. We have not been able to locate his type material. The generic diagnosis has been given above. The diagnoses and illustrations of the six species are uneven. The first three were based on Jurassic material, from Solnhofen lithographic limestone.

The first species, *M. clavata*, was not illustrated, but reference was made to Brongniart's (1828) *Fucoides encoelioides* (Ekdale *et al.* 1984, fig. 1-1, top left). Sternberg disagreed with Brongniart that the species was closely related to the recent alga *Encoelium bullosum*, and therefore altered its species name. Sternberg's diagnosis for *M. clavata* is a shortened version of Brongniart's (1828, p. 55) for *F. encoelioides*. Brongniart's sample was collected in the Jurassic limestone of Solnhofen and probably comprised poorly preserved plant remains, as did Sternberg's fossils; in fact the trace fossil '*Muensteria*' of authors is unknown in the Solnhofen sediments, which were deposited in largely anoxic environments (F. T. Fürsich, pers. comm. 1984).

Sternberg's second species, *M. vermicularis*, differs from *M. clavata* only in being solitary. The illustration supports the description, showing a particularly unimpressive specimen. The palaeobotanist Andrews (1955, p. 191) chose this to be the type species of the genus, identifying the plant as an 'alga?'

The third species, *M. lacunosa*, appears to be a coprolite, and was considered as such by Schenk (1864, p. 296). The remaining three species derive from Vienna and are branched. *M. hoessii* (Sternberg, 1833, pl. 6, fig. 4; cf. text-fig. 4) appears to be a *Chondrites*, and its diagnosis describes it as dichotomous. *M. flagellaris* Sternberg, 1833, pl. 8, fig. 3, also strongly resembles *Chondrites*; his diagnosis distinguishes it on the basis of short side branches. Finally, *M. geniculata* has a characteristic spreite and has been designated type ichnospecies of *Hydrancylus*.



TEXT-FIG. 4. *Chondrites hoessii* (Sternberg, 1833), MGUH 17555, from the same horizon as *Taenidium satanassi* ichnosp. nov., showing the faintly meniscate fill and primary successive branching. Scale, 1 cm.

We conclude that Sternberg's genus has no single claim for validity, so *Muensteria* must be considered unavailable as an ichnogenus. As a plant taxon it is probably a *nomen dubium*.

The next author to use *Muensteria* was Schafhäütl (1851) whose *M. annulata* is a clearly branched trace fossil (apparently in a primary successive manner) but extremely poorly defined.

Fischer-Ooster (1858) greatly complicated the issue by erecting three subgenera for *Muensteria*. The only one that concerns us is *M. (Keckia)*, into which he placed *M. annulata* Schafhäütl and, mysteriously as a synonym, *K. annulata* Glocker, 1841. Also in *M. (Keckia)* he placed Sternberg's *M. hoessii*.

Heer (1877) further confused matters by erecting a simple branched species, *M. antiqua*, and by introducing a further genus, *Taenidium*, that mainly differs from *Muensteria* in possessing menisci (Heer 1877, p. 117), although Heer's illustration of *M. hoessii* (1877, pl. 69, fig. 3) clearly shows menisci.

Nereites MacLeay, 1839

[= *Phyllodocites* Geinitz, 1867; *Scalarituba* Weller, 1899; *Neonereites* Seilacher, 1960; *Maldanidopsis* Plička, 1973.]

Discussion. The close relationship between *Nereites*, *Neonereites*, and the meniscate burrow *Scalarituba* was demonstrated by Seilacher and Meischner (1964). Although these ichnogenera have highly distinctive morphologies, they appear to be merely preservational variants of the same behavioural expression (Ekdale *et al.* 1984, figs. 2–5). This equivalence was emphasized by Chamberlain (1971) and Seilacher (1983).

Thus, although *Scalarituba* has the appearance of a simple meniscate structure corresponding more or less to the concept of *Muensteria* of authors, in fact it is merely the cylindrical septate axis of a more complex structure, as is demonstrated by the common presence of a more or less visible halo. In Frey *et al.*'s (1984, fig. 1A) illustration of Weller's holotype of *S. missouriensis*, this halo is visible and corresponds to the disturbance zone surrounding the central meniscate fill that is emphasized in *Nereites* preservation. Seilacher (1983) advocated placing *Scalarituba* and *Neonereites* in synonymy with *Nereites*, thus completing the trend started by Chamberlain (1971, 1978). The more important ichnogenera included by Seilacher in this group of synonyms are *Scalarituba*, *Phyllodocites*, *Neonereites*, and *Helminthoida*; however, the last-named has a non-septate central fill and therefore is distinct.

Keckia Glocker, 1841

Discussion. Glocker (1841) erected *Keckia annulata* on the basis of two specimens from Upper Cretaceous sandstone (Germany). Despite his beautiful colour plate (1841, pl. 4), it is not clear what the genus comprises. Described in terms of plants and compared to lycopodiaceans, Glocker (1841, pp. 318–319) considered the crescent-shaped rings visible in parts of his specimens to be atypical of fucoid structures. On this basis, he distinguished his genus from *Muensteria* Sternberg. Furthermore, *K. annulata* was considered to be more densely branched than *M. hoessii*. From his plate the branching pattern appears to be primarily successive in most cases. However, the structure of the fossil varies so extensively from part to part that possibly it is composed of intersections of several distinct taxa. Although one branch of the larger specimen and the small second specimen appear to be unwallied meniscate burrows, we regard this confusingly based ichnotaxon as a *nomen dubium*.

Scolicia de Quatrefages, 1849

[*Bolonia* Meunier, 1886; *Taphrhelminthopsis* Sacco, 1888; *Subphyllochorda* Götzing and Becker, 1932.]

Discussion. Seilacher (1955, 1983) stated that the morphological differences between the ichnogenera listed above (among many others) represent various preservational expressions of the same fundamental type of burrowing activity. *Bolonia* and *Subphyllochorda* were mentioned by Häntzschel (1962, 1965, 1975), together with other ichnotaxa, as belonging to the 'Scolicia group' even if not classifiable as true synonyms, but *Taphrhelminthopsis* was described separately. Häntzschel (1975), Książkiewicz (1977), Smith and Crimes (1983), and others have shown by means of sketches the possible relationship between biostratinomic processes and the morphology of the same structures belonging to the *Scolicia* group, to which the effects of preservation must be added (D'Alessandro 1980, fig. 3). Thus the ichnogenetic names under discussion appear to reflect different taphonomic features of the same type of trace, and should therefore be placed in synonymy. Nevertheless, some authors (e.g. Książkiewicz 1977; Crimes 1977; Smith and Crimes 1983) preferred to retain distinct ichnogenetic names even in cases where such names could with reasonable safety be ascribed to taphonomic variation.

Thus we consider the ichnogenus *Scolicia* to include those trace fossils in which the sediment is backfilled to form densely packed lamellae bearing one or two parallel ridges, strings, or grooves lying below or within the lamellar fill. The concave epirelief expression takes the form of a bilaterally symmetrical laminated trail divided into two or three lobes by longitudinal grooves; as a slightly convex epirelief variant, *Scolicia* displays a plait-like pattern (Książkiewicz 1977, fig. 24f; Smith and Crimes 1983, fig. 4d). *Scolicia* always lacks the median vertical discontinuity plane that is characteristic of *Curvolithus* and the distinctively different *Gyrochorte* (see Heinberg 1973).

Psammichnites Torell, 1870

[= *Olivellites* Fenton and Fenton, 1937a; *Aulichnites* Fenton and Fenton, 1937b;
? *Laminites* Ghent and Henderson, 1966.]

Discussion. The original material of *Olivellites* was described (Fenton and Fenton 1937a) as a meandering trace fossil preserved in convex epirelief. It appears to be bilaterally symmetrical and divided into two zones by a median solid string. The fill is composed of concave thin backfill lamellae; in the string itself, the sediment was described as 'not closely packed' (Fenton and Fenton 1937a, p. 453).

The original specimen of *Aulichnites* is a full relief structure that seems to differ from *Olivellites* exclusively in lacking the string; thus it appears to be divided into two lobes by a single median furrow. Hakes (1977) demonstrated that the lower surface of the original specimen of *Aulichnites* is regularly convex. It is reasonable to suppose, therefore, that both ichnogenera represent preservational variants of the same structure. Furthermore, the morphology of *Olivellites* closely corresponds to that of *Psammichnites* (see Häntzschel 1975, fig. 62, 2c), of which we consider it a junior synonym.

In its original diagnosis, *Laminites* was described as a subcylindrical backfilled trace having concave or biconcave laminae alternately dark and light; these laminae were interpreted as having been produced by separate packets of faeces extruded into the burrow (Ghent and Henderson 1966). The trace fossil is preserved as convex epirelief. Further examples of such a structure were given by Chamberlain (1971, 1978). In longitudinal section it is not always possible to distinguish *Scolicia* from *Laminites*. At present, our knowledge of this form is still limited as regards its morphological range and preservational variants; the construction of its under surface, so critical in the *Scolicia* group, is unknown. Therefore, provisionally we consider *Laminites* to be a synonym of *Psammitichnites*, until its construction is better understood.

Taenidium Heer, 1877

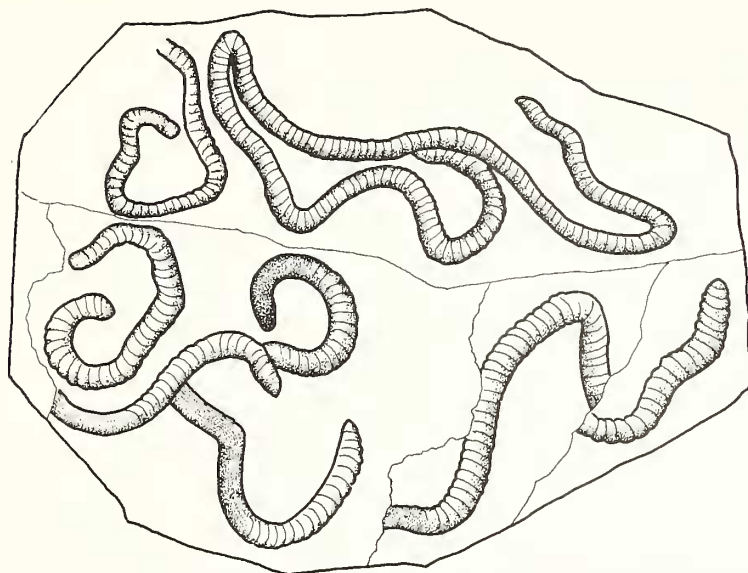
- non 1823 *Fucoides encoelioides* Brongniart, p. 55, pl. 6, fig. 4.
 non 1833 *Muensteria* Sternberg, pp. 31–32, pl. 6, fig. 4; pl. 7, fig. 3.
 1858 *Muensteria hoessii* (non Sternberg) Fischer-Ooster (*partim*), p. 62, pl. 16, fig. 4.
 1877 *Taenidium* Heer (*partim*), p. 117, pl. 45, figs. 9 and 10b; pl. 50, figs. 1 and 2.
 ? 1877 *Muensteria flagellaris* (non Sternberg) Heer, pl. 66, figs. 4 and 5.
 1877 *Muensteria hoessii* (non Sternberg) Heer, p. 164, pl. 69, fig. 3.
 1947 *Scolecocoprus* Brady, p. 471, pl. 69, fig. 1.
 1958 *Muensteria* Sternberg; Seilacher, p. 1071, table 2, fig. 28.
 1958 *Muensteria hoessii* (non Sternberg) Seilacher, p. 1071, table 2, fig. 40.
 1962 *Muensteria* Sternberg; Häntzschel (*partim*), p. 205.
 1962 *Muensteria hoessii* (non Sternberg) Seilacher, p. 229, pl. 2, fig. 6.
 1964 *Muensteria* Sternberg; Seilacher, p. 309, fig. 7 (27), table 1 (27).
 1971 *Taenidium serpentium* Heer; Chamberlain, p. 241, pl. 32, fig. 10.
 1974 *Muensteria* Sternberg; Fürsich (*partim*), p. 34, fig. 29a.
 1974 *Muensteria* Sternberg; Heinberg, p. 17, figs. 1B and 9C.
 ? 1977 *Keckia* cf. *hoessii* (Sternberg); Książkiewicz, pl. 3, fig. 12.
 1977 *Muensteria* Sternberg; Chamberlain (*partim*), p. 14, figs. 2E and 5F.
 1977 *Taenidium serpentium* Heer; Chamberlain, p. 18, figs. 2A, H, 3F, I, 7A.
 1983 *Muensteria* Sternberg; Wetzel (*partim*), p. 290, fig. 2.
 non 1984 *Muensteria* Sternberg; Bracken and Picard, p. 485, fig. 12.
 1984 *Muensteria* Sternberg; Pemberton and Frey, p. 291.
 1985 *Muensteria* Sternberg; Frey and Howard, pp. 378–379, figs. 10.12, 16.3(B), 19.6.
 1985 *Entradichmus* Ekdale and Picard, p. 8, pl. 2A, B.
 1986 *Muensteria* ichnosp. D'Alessandro *et al.*, p. 299, fig. 5B.

Preliminary remarks. *Taenidium* is generally considered today to be a branched meniscate structure (Häntzschel 1975, fig. 70.1). However, the terms in which the genus was introduced originally (Heer 1877) are very similar to the original diagnosis of *Muensteria* (see introduction above). Its original Latin diagnosis is unsatisfactory owing to the linguistic bias caused by an algal interpretation.

Heer's first species, *T. serpentinum* (text-fig. 5) has been designated subsequently by Andrews (1955, p. 243) as type species of 'alga?'; and by Häntzschel (1975, p. 112) as type species of a branched, root-like system of burrows, even though this species is unbranched. Heer's diagnosis is as follows: '*T. fronde simplicis, valde incurvata, serpentina, 3 mm lata, evidenter articulata, articulis 1 mm longis*'. (Simple *Taenidium* frond, strongly bent, serpentine, 3 mm wide, evidently articulated, the joints 1 mm long.)

Heer's second and third species, *T. gillieronii* and *T. convolutum*, are also unbranched and differ only in size from the type species. Their illustrations show no true branching, but indicate superficial wrinkling and evenly spaced menisci (Heer 1877, pl. 45, figs. 9 and 10b; pl. 50, figs. 1 and 2). *Taenidium* is thus meniscate and unbranched, and on this basis it would be logical to consider *Taenidium* to be the first valid name for *Muensteria* of authors. These three species were founded on Swiss Jurassic material.

Later in the same work, Heer (1877, p. 162) illogically named a strongly branched, radiating, septate structure *T. fischeri* and he listed *M. annulata* of Schafhäütl (1851) among its synonyms. Afterwards



TEXT-FIG. 5. *Taenidium serpentinum* Heer, 1877. Redrawn from Heer's pl. 45, fig. 9. About natural size.

(Heer 1881) he founded a new species, *T. lusitanicum*, for a palmate form. These later species differ radically from the original ones in possessing ramification. Nevertheless, Häntzschel (1975, p. 112) pronounced *T. fischeri* the 'most typical', and confirmed the general tendency to consider *Taenidium* a much-branched ichnogenus. As pointed out above, however, this is not the original connotation.

Emended diagnosis. Unlined or very thinly lined, unbranched, straight or sinuous cylindrical burrows containing a segmented fill articulated by meniscus-shaped partings.

Type species. *T. serpentinum* Heer, 1877.

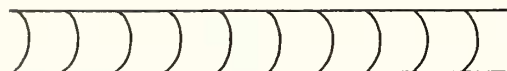
Discussion. Fragments of *Cladichnus* that do not show their characteristic branching may be confused with short lengths of *Taenidium*. However, individual branches of *Cladichnus* commonly are less winding, have stronger annulation or moniliform development, or they may possess cone-in-cone articulations, and consequently have a less linear border than *Taenidium*. Many species in the literature are based on fragments too small to display sufficient characteristics for identification.

Nereites, when only its central axis is preserved, may be mistaken for *Taenidium*; the disturbance zone around *Nereites* is revealed, however, in such cases where two burrows cross (Frey *et al.* 1984, fig. 1A).

Taenidium differs from *Ancorichnus* in lacking a 'distinct mantle' (Heinberg 1974). However, on the basis of illustration, the trace fossils *A. coronus* (Frey *et al.* 1984, figs. 1D, E and 3) and *A. capronus* (Howard and Frey 1984, figs. 2 and 3A, B) appear to be thinly walled and thus less distinct from *Taenidium* than from *A. ancorichnus*. McCarthy's (1979, p. 263, fig. d) *Keckia*, a trace fossil having 'poorly defined walls', was compared to Frey and Howard's (1970, fig. 8a) 'chevron trails'; but Frey and Howard (1985) placed the latter in synonymy with *A. capronus*.

There is a close resemblance between *Taenidium* and *Beaconites*. When the latter is better known it may be revealed as a junior synonym of *Taenidium*. However, differences such as the irregularity and flattened shape of the menisci, and the large size of the structures, may be used to perpetuate the ichnospecies of *Beaconites*.

The morphology of *Imbrichnus protuberans* in bedding plane view (Marintisch and Finks 1982, pl. 5, fig. 1) resembles *Taenidium* in the same view. Moreover, the vertical structure through the



T. serpentinum



T. cameroneensis



T. satanassi

TEXT-FIG. 6. Essential features of the three valid ichno-species of *Taenidium*.

mid-line of *I. protuberans* (their pl. 5, fig. 2) shows imbricate structure that may represent the lower half of the simple meniscate fill of *Taenidium*. On the other hand, *I. wattonensis* Hallam has an imbricated structure (Hallam 1970, p. 198) that does not take the form of hemispherical menisci.

Interpretation. Different authors have interpreted active fill of burrows in different ways. Some have assumed that the material packed behind the animal on its way through the sediment is entirely faecal, having passed through the gut (Fürsich 1974, p. 35). Others have emphasized that the sediment is transported around the body during the animal's progress through the substrate (e.g. Heinberg 1974, p. 18; Bromley and Asgaard 1975, p. 276). The alternation of two types of sediment that produces the meniscus structures may arise from physical sorting of the sediment, producing alternate fine-grained and coarse laminae (Stanley and Fagerstrom 1974, p. 74), or from a combination of ingestion and external transport (Bromley and Asgaard 1979; Pemberton and Frey 1984). It seems reasonable in most cases to regard the sediment packages that resemble lithologically the surrounding sediment as non-ingested, and the alternating compressed fine-grained material as coprolitic in origin. The proportions of these two components vary in different types of burrow fills.

Included species. We recognize three valid ichnospecies (text-fig. 6) while four other ichnospecies must be regarded as dubious: type ichnospecies — *T. serpentinum* Heer, 1877; other ichnospecies — *T. cameroneensis* (Brady, 1947) and *T. satanassi* ichnosp. nov.; dubious ichnospecies — *Muensteria cretacea* Heer, 1877, *T. carboniferum* Sacco, 1888, *T. maeandriiformis* Müller, 1966, and *M. planicostata* Książkiewicz, 1977.

Taenidium serpentinum Heer, 1877

Text-figs. 6A and 7

- ? 1858 *Muensteria hoessii* Fischer-Ooster (*partim*), p. 62, pl. 16, fig. 4 (*non* fig. 5).
- 1877 *Taenidium serpentinum* Heer, p. 117, pl. 45, figs. 9 and 10b.
- 1877 *Taenidium gillieronii* Heer, p. 117, pl. 50, fig. 1.
- 1877 *Taenidium convolutum* Heer, p. 117, pl. 50, fig. 2.
- ? 1877 *Muensteria flagellaris* Heer (*non* Sternberg), pl. 66, figs. 4 and 5.
- + 1877 *Muensteria hoessii* Heer (*partim*), p. 164, pl. 69, fig. 3 (*non* pl. 66, fig. 6).
- + 1958 *Muensteria hoessii* Heer; Seilacher, p. 1071, table 2, fig. 40.
- + 1962 *Muensteria hoessii* Heer; Seilacher, p. 229, pl. 2, fig. 6.
- 1971 *Taenidium serpentinum* Heer; Chamberlain, p. 241, pl. 32, fig. 10.
- + 1977 *Muensteria* cf. *hoessii* Sternberg; Chamberlain (*partim*), p. 14, figs. 2E and 5F.

Diagnosis (emended). Serpentine *Taenidium* having well-spaced, arcuate menisci; distance between menisci about equal to or a little less than burrow width. External moulds may show slight annulation corresponding to menisci, or fine transverse wrinkling. Secondary subsequent branching and intersections occur. Boundary sharp, lining lacking or insignificant.



TEXT-FIG. 7. *Taenidium serpentinum* Heer, 1877, MGUH 17552, from the Lower Jurassic Gule Horn member, Neill Klintner Formation of Jameson Land, East Greenland. Scale, 2 cm.

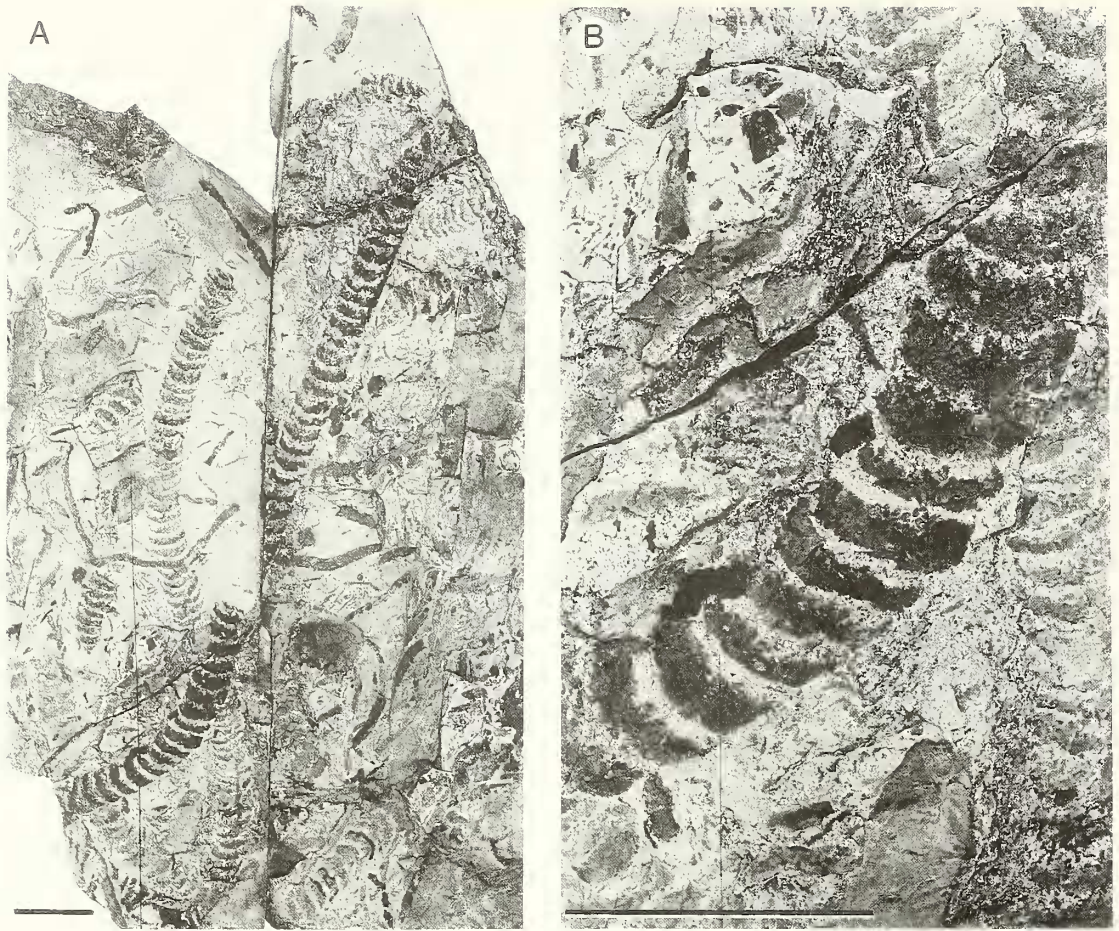
Type area and age. Switzerland, Jurassic.

Discussion. This name is useful for the common form of 'Muensteria'; for example, in the Lower Jurassic of East Greenland (Surlyk *et al.* 1971, p. 29; Heinberg and Birkelund 1984, *partim*) (text-fig. 7), where the form is generally preserved in full relief in micaceous sandstone. The wall of this trace fossil is sharp and possibly lined by an extremely thin film of clay or mica grains. Similarity with the illustrations of Heer (1877, pl. 50, figs. 1 and 2) is striking.

The citations in the synonymy list prefixed with a cross (+) may represent a distinct ichnospecies. As far as can be judged from illustrations, these burrows are larger and the fill has more densely alternating packets of two types of sediment than the typical *T. serpentinum*. Nevertheless, as we are dealing with incomplete burrows, shown only in longitudinal section, we prefer temporarily to include them in *T. serpentinum*.

If they *are* considered to comprise a separate ichnospecies, the once commonly used specific name 'hoessii' would not be suitable because it was employed by Sternberg for two different structures: a *Chondrites* (1833, pl. 6, fig. 4) comparable with our text-fig. 4, and an incomplete burrow (1833, pl. 7, fig. 3) of doubtful interpretation. The name, therefore, could be employed in the ichnogenus *Chondrites* as *C. hoessii* (Sternberg). Fischer-Ooster (1858, pl. 16, figs. 4 and 5) applied the name to meniscate traces, one of which cannot be included in *Taenidium*, being bordered by a wide band, and the other being scarcely significant. Heer (1877) determined two different structures as *M. hoessii*: one that could be an incomplete *Spirophycus* (pl. 66, fig. 6) and another that suggests a real *Taenidium*. *M. hoessii* is thus a *nomen catastropicum*, as is the genus itself.

Häntzschel's (1972) *T. carbonicum* (a *lapsus* by Häntzschel for *T. carboniferum* Sacco) has an indistinct dark zone surrounding a well-preserved meniscate fill. The zone appears to cut other burrow fills, indicating that this structure should be referred instead to *Nereites*.



TEXT-FIG. 8. *Taenidium satanassi* ichnosp. nov. in cleavage relief preservation. A, B, MGUH 17553, specimen containing the holotype (most conspicuous, longest preserved burrow, detailed in B); the other meniscate structures are paratypes. C, D, MGUH 17554, paratypes. Scale, 2 cm.

The non-marine *Entradichnus meniscus* may belong here, although the menisci appear to be closely spaced and rather flat, as in *B. antarcticus* Vialov.

Taenidium cameronensis (Brady, 1947)

Text-fig. 6B

1947 *Scolecocopus cameronensis* Brady, p. 471, pl. 69, fig. 1.

? 1979 *Keckia* sp. McCarthy, p. 363, fig. 3c.

Diagnosis (emended). *Taenidium* having intermeniscate segments generally longer than wide, and deeply concave menisci; secondary successive branching and intersection occur.

Type area and age. Arizona, probably Permian.

Discussion. This ichnospecies is separated from *T. serpentinum* on the basis of its distinctly longer packets of sediment between successive menisci in the backfill. The arc of the meniscus is also much



deeper, tending towards parabolic, so that each packet nests around the next. Hitherto, all references to this ichnospecies have been from shallow water settings (e.g. Decourten 1978, p. 491, fig. 1).

Taenidium satanassi ichnosp. nov.

Text-figs. 2, 3, 6C, 8A-D, 9

1958 *Muensteria* Seilacher, p. 1071, table 2, fig. 28.

1986 *Muensteria* ichnosp. D'Alessandro *et al.*, p. 299, fig. 5B.

Derivation of name. *Satanassus*, Satan, after whom the type locality is named, a river that had disastrously unpredictable floods.

Type material. Holotype, MGUH 17553 (text-fig. 8A, B) and paratypes, MGUH 17553, 17554 (text-fig. 8A, C, D) deposited in the Geological Museum, University of Copenhagen, Denmark; from Fiumara Satanasso, Villapiana, near Sibari, southern Italy; Saraceno Formation, middle-upper Eocene.

Other material. Several specimens from the lower part of the Saraceno Formation, deposited in the Department of Geology and Geophysics, University of Bari, and Department of Earth Science, University of Calabria.



TEXT-FIG. 9. Sketch of an example of *Taenidium satanassi* ichnosp. nov., convex hyporelief, showing the tightest observed curvature.

Diagnosis. Weakly sinuous to nearly straight *Taenidium*, the fill consisting of evenly alternating meniscus-shaped packets of two types of sediment, of more or less equal thickness; sediment packets considerably shorter than wide.

Description. The burrows lie parallel or weakly inclined to bedding. The fill in the type material is very characteristic, the packets of sediment being alternately dark and pale. One of these two types of sediment, usually the dark material, is clearly pelleted and grades on the concave side into the other type of sediment which, in turn, is closely similar to the surrounding sediment. The packets of unpelleted sediment are usually a little thinner than the pelleted segments, or may reach equal size. The curvature of the meniscus is relatively wide, and the sediment packets consequently do not partially enclose or wrap around each other. In thin section the unpelleted sediment packets seem to run continuously into the surrounding sediment without interruption, but on weathered surfaces a very faint colour difference and boundary interface can be detected. There is thus no detectable wall lining or special grain orientation at the junction.

The burrows have an average width of 8.82 ± 0.73 mm ($n = 33$), showing an observed range of 4–14 mm and a unimodal size-frequency distribution. The type material is highly compacted; it is mainly preserved in (now flattened) cleavage relief on upper surfaces or, more rarely, in semirelief on soles.

Discussion. *T. satanassi* differs from the other ichnospecies in its weakly arcuate menisci, more or less equally sized packets of alternating sediment type, obviously pelleted form of the fill (text-fig. 8), straight-sided boundary, and little-winding course. Greater affinity exists between *T. satanassi* and the forms prefixed by a cross in the *T. serpentinum* synonymy. The main differences here are in the more or less equal quantities of alternating sediment types in the former, and the more arcuate menisci of the latter so that each packet partially wraps around the next.

T. satanassi resembles *B. antarcticus*. However, the latter's backfill appears to have alternating sediment units of unequal thickness; furthermore, the septa appear flattened at the centre but curve more or less abruptly as they approach the boundary (Vialov 1962; Gevers *et al.* 1971, p. 84; Bradshaw 1981, p. 631), whereas those of *T. satanassi* curve in a regular arc. Moreover, *B. antarcticus* seems to have a wall.

T. satanassi also resembles the meniscate trace fossil of Stanley and Fagerstrom (1974, figs. 6–8), recently included in *Ancorichnus* by Frey *et al.* (1984). However, a clear difference can be observed in the arrangement of the menisci when the direction of the burrow changes. In *Taenidium* the diameter of the structure remains constant and the menisci tend to keep parallel to each other, fanning out slightly where the burrow bends (text-fig. 9); when the traces described by Stanley and Fagerstrom (1974) bend, the menisci are oriented at variable angles and truncate one another. Thus, this character may be the morphological expression of a distinct burrowing pattern. A different form of irregular meniscate development is shown by the form referred to as *Muensteria* ichnosp. by Bromley and Ekdale (1984, figs. 3B and 4A–C) in chalk.

Dubious ichnospecies of *Taenidium*

M. cretacea Heer, 1877, p. 144, is characterized by extremely deeply concave menisci that divide the cylindrical structure into pale and dark densely alternating units; each unit wraps around several of the following. It is not easy to evaluate this fragment; it may represent part of a body fossil.

The original description of *T. carboniferum* Sacco, 1888, p. 162, includes '*Frons . . . moniliformis, subcylindrica, . . . annulosa . . . articulata; articuli crassi, subelliptici, inter se profunde disjuncti . . .*'; Sacco added that the rounded segments are separated by 0.5 mm. This form was included in the algal genus '*Taenidium*', having segments distinctly separated; on this basis, we hesitate to consider it a *Taenidium* and suggest that it could belong rather to the ichnogenus *Hormosiroidea*.

The single specimen *T.?* *maeandriiformis* Müller, 1966, resembles *T. serpentinum* in its winding course and size. The flattened fill consists of segments about as wide as long, separated by fairly flat menisci, distinguishing it from *T. camaronensis*. The meandering course and mode of preservation are reminiscent of *Nereites*, but no lateral zones are visible. Owing to this uncertainty, therefore, we reserve judgement on this ichnospecies. This name was used again by Plička (1973) who described a large example of unquestionable *Nereites*, but considered it to be the body fossil of a worm and assigned it to a new genus, *Maldanidopsis*.

Muensteria planicosta Książkiewicz, 1977, was founded on a winding meniscate trace fossil, preserved as hyporelief; the menisci are regularly arcuate and very dense (Książkiewicz 1977, p. 122, pl. 13, fig. 1). The trace bends abruptly through a right angle, showing changes in width, characters that are atypical of *Taenidium* but reminiscent of '*Laminites*'.

Scoyenia White, 1929

Discussion. The morphology and ethology of this trace fossil and its environmental significance have been analysed recently (Bromley and Asgaard 1979; Frey *et al.* 1984). Straight or gently curved endogenic structures, limited by distinct boundaries and ornamented with external longitudinal striae, are included here. The burrow contains a conspicuously meniscate backfill. *Scoyenia* is an unbranched burrow that commonly exhibits cross-overs, intersections, or secondary successive branching (Bromley and Asgaard 1979, figs. 9A and 10).

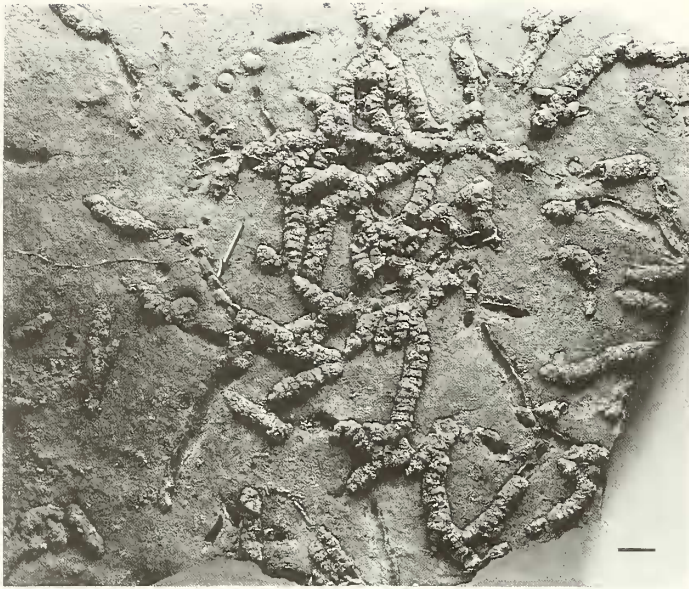
Beaconites Vialov, 1962

Discussion. The original description of *B. antarcticus* Vialov, 1962, was extremely weak. Re-examination of topotypic material by Bradshaw (1981) has improved our understanding of this form but, owing to the high degree of weathering, details of the burrow boundary are unclear. In the type ichnospecies, Bradshaw (1981, p. 630) wrote of 'a poorly developed sand lining' and this is supported by her fig. 15. The illustration by Gevers *et al.* (1971, pl. 18, fig. 3) similarly shows a boundary ridge in cross-section, interpretable as a wall structure. The sediments were apparently deposited in a non-marine environment. Giant meniscate structures have also been assigned to the ichnogenus *Beaconites* (e.g. Gevers *et al.* 1971; Ridgeway 1974; Pollard 1976) and these have been placed in *B. barretti* by Bradshaw (1981). The description of this ichnospecies also implies a weak wall structure (Gevers *et al.* 1971, p. 84; Bradshaw 1981, p. 631) although in the illustrations the wall appears to be composed only of the superposed nested menisci rather than being a discrete structure. This also appears to be the case in the giant burrows illustrated by Allen and Williams (1981). The vertical orientation of many of these continental occurrences (Allen and Williams 1981; Bracken and Picard 1984) may indicate an escape element that would further separate them from normal '*Muensteria*' of authors.

Examination of unweathered material will be necessary to clarify the relationship between *Beaconites*, *Taenidium*, and *Ancorichnus* (as emended by Frey *et al.* 1984).

Phoebichnus Bromley and Asgaard, 1972

Discussion. The strongly walled *Phoebichnus trochoides* is distinguished by its special wall construction and radiating morphology (Bromley and Asgaard 1972; Bromley and Mørk 1984).



TEXT-FIG. 10. MGUH 17556, a branching, annulated, meniscate structure in hyporelief, from the Upper Permian, Domkirken, Scoresby Land, central East Greenland (L. Stemmerik Collection); arrow indicates the meniscate fill where the thick wall is broken away. Scale, 2 cm.

Ancorichnus Heinberg, 1974

Discussion. Among the unbranched meniscate trace fossils, *Ancorichnus* is distinctive in having a well-developed, unornamented wall structure. In *A. coronus* Frey *et al.*, 1984, and *A. capronus* Howard and Frey, 1984, the wall material is far less well developed than in the type ichnospecies *A. ancorichnus*, and their ichnogenetic placing is therefore questionable.

Branched septate burrow having wall structures

Discussion. There is a distinctive group of branched trace fossils that has a resemblance to *M. annulata* Schafhäütl, possessing a complicated and thick wall structure. These walled trace fossils have received heterogeneous taxonomic treatment, and it is not clear to which ichnogenus or ichnogenera they should be referred (but see D'Alessandro, Bromley, and Stemmerik, in prep.).

As in the case of the *Nereites/Scalarituba/Neonereites* group, the walled, branched, septate burrows have a complicated structure that is capable of producing widely varying morphologies according to the stratigraphic position and taphonomic processes. Thus, in semirelief, the annulated or striated external sculpture of the walling material is emphasized (e.g. D'Alessandro 1982, pl. 40), whereas only in axially sectioned material is the septate central backfill visible (text-fig. 10).

Fucusopsis was used by Książkiewicz (1970, 1977) for structures of this kind, and *Radionereites* by D'Alessandro (1982). Neither ichnogenus has been demonstrated to have septate interiors, however. Pemberton and Frey (1982) placed *Fucusopsis* in synonymy with the non-septate *Palaeophycus*. Topotypic material of *Radionereites* (kindly supplied by M. Gregory) confirms that D'Alessandro's form does not belong to this ichnogenus.

Cladichnus ichnogen. nov.

- 1858 *Muensteria (Keckia) annulata* Schafhäütl; Fischer-Ooster (*partim*), p. 37, pl. 7, fig. 4 (*non fig. 3 = Chondrites*); pl. 12, fig. 8.
- 1877 *Taenidium fischeri* Heer, p. 162, pl. 67, figs. 1-5, 7.
- 1881 *Taenidium lusitanicum* Heer, p. 12, pl. 20.
- 1887 *Muensteria annulata* Squinabol, p. 554, pl. 17, fig. 3.

- 1947 *Saportia striata* Wilckens (*non* Squinabol), p. 41, pl. 7, fig. 3.
 1947 *Taenidium lusitanicum* Heer; Wilckens, pp. 41–45, pl. 6, figs. 1 and 2; pl. 7, fig. 1.
 1955 *Taenidium fischeri* Heer; Seilacher, fig. 5.83.
 1958 *Taenidium fischeri* Heer; Seilacher, p. 1073, table 3, fig. 48.
 1962 *Taenidium* Heer; Häntzschel, fig. 136.2.
non 1971 *Taenidium annulatum* Schafhäütl; Chamberlain, pl. 32, fig. 12.
 1975 *Taenidium* Heer; Häntzschel (*partim*), p. 112, fig. 70.1.
 1977 *Taenidium fischeri* Heer; Książkiewicz, pl. 5, fig. 3.
 1978 *Taenidium* Heer; Kern, p. 249, fig. 8f.
 1983 *Taenidium* ichnosp. Pedersen and Surlyk, p. 53, fig. 12.
 1986 *Taenidium annulatum* Schafhäütl; D'Alessandro *et al.*, p. 300, fig. 5c.

Derivation of name. Greek *klados*, branch.

Type species. *Cladichmus fischeri* (Heer, 1877).

Diagnosis. Annulated or monilliform burrow fills composed of meniscus-shaped segments, comprising primary successively branched and radiating systems; wall lining lacking or very thin.

Discussion. These meniscate burrow fills have a smooth outer sculpture and are annulated or monilliform. They show primary successive branching, generally at acute angles, and the menisci are concave towards the proximal direction. Branching may produce a radiating plan (*C. fischeri*; text-fig. 11), or be palmate (*C. lusitanicum*) or dendroid (*Taenidium* ichnosp. of Pedersen and Surlyk 1983). It is uncertain whether or not the type species has a wall structure. If it has, it is no more than a film-like or insignificant skin. In the figure of Heer (1877, pl. 67, fig. 6) in which a wall is indicated, the illustration is said to represent the condition 'in life' (as an alga!) and is therefore a spurious reconstruction. Heer (1881, pl. 20) and Pedersen and Surlyk (1983, fig. 12c) indicated a very thin wall material.

Cladichmus fischeri (Heer, 1877)

Text-fig. 11

- ? 1858 *Muensteria (Keckia) annulata* Schafhäütl; Fischer-Ooster (*partim*), p. 37, pl. 7, fig. 4 (*non* fig. 3); pl. 12, fig. 8.
 1877 *Taenidium fischeri* Heer, p. 162, pl. 67, figs. 1–5, 7.
 1887 *Muensteria annulata* Squinabol, p. 554, pl. 17, fig. 3.
 1955 *Taenidium fischeri* Heer; Seilacher, fig. 5.83.
 1958 *Taenidium fischeri* Heer; Seilacher, p. 1073, table 3, fig. 48.
 1962 *Taenidium* Heer; Häntzschel, fig. 136.2.



TEXT-FIG. 11. Field photograph of *Cladichmus fischeri* (Heer, 1877) from the same horizon as the *Taenidium satanassi* material. Scale, 1 cm.

- 1975 *Taenidium* Heer; Häntzschel (*partim*), p. 112, fig. 70.1.
 1977 *Taenidium fischeri* Heer; Książkiewicz, pl. 5, fig. 3.
 1978 *Taenidium* Heer; Kern, p. 249, fig. 8F.
 1986 *Taenidium annulatum* Schafhäütl; D'Alessandro *et al.*, p. 300, fig. 5c.

Diagnosis. Radiating and primary successively branched *Cladichnus*.

Discussion. *Muensteria annulata* Schafhäütl, 1851, is not listed as a synonym because it is a dubious structure. In the illustration it closely resembles the branching, septate, walled burrow, but it is not clear whether or not a wall structure is present. Heer considered *M. annulata* a synonym of his *T. fischeri*.

Most *Cladichnus* show a tendency to radial development. In some examples (text-fig. 11) the radiating burrow fills are generally straight, originate at several levels from a central shaft, and show little or no subsequent branching. In others, branching of the radial elements may occur but to what extent is hard to discern. In early illustrations suggesting algal origin (e.g. Heer 1877, pl. 67, fig. 1), simultaneous filling is suggested, but it is probable that most such branching is in fact intersection, compacted close application of elements, and primary subsequent branching. In lower Tertiary material from Italy (text-fig. 11), extreme compaction has given the impression of true branching in cases where intersection can be demonstrated by careful inspection.

Other ichnospecies of *Cladichnus*

We place *T. lusitanicum* Heer, 1881, temporarily in *Cladichnus* owing to its primary successive branching pattern and meniscate fill. However, its palmate form is highly distinctive and represents a fundamentally different burrowing behaviour from the radiating forms. Pedersen and Surlyk's (1983) *Taenidium* ichnosp. has a root-like branching pattern and appears to be a distinct ichnospecies of *Cladichnus*.

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